

## NOTES ON NEOTROPICAL ANT-PLANTS

### I. CECROPIA ANGULATA, SP. NOV.

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(WITH PLATE XV AND EIGHT FIGURES)

#### Introduction

In a previous paper (1) the writer discussed the significance of the anatomical peculiarities of a number of Ethiopian ant-plants. So many features of unusual interest were encountered in studying these plants, that it seemed desirable to extend the scope of the investigation, and to include certain neotropical myrmecophytes for comparative purposes. With this end in view, the writer spent the summer of 1920 at William Beebe's Tropical Research Station in British Guiana, where the following ant-plants (*Tococa aristata* Benth., *Triplaris surinamensis* Cham., *Tachigalia paniculata* Aubl., *Cordia nodosa* Lam., and *Cecropia angulata*, sp. nov.) grow in close proximity to the laboratory.

Since the publication of SCHIMPER'S (8) much quoted investigations, *Cecropia adenopus* Mart. has been considered one of the most classical illustrations of myrmecophytism. SCHIMPER interpreted the "Müllerian food bodies" and the "prostomata" of this ant-plant as adaptations for enlisting the services of an aggressive army of Aztecas, which protect their host against the attacks of the destructive, leaf cutting, Attine ants; a conclusion that has been assailed by VON IHERING (4), ULE (9), RETTIG (7), FIEBRIG (3), and other critics of the BELT-DELPINO theory of myrmecophily. In view of the important rôle that has been assigned to *C. adenopus*, in discussions concerning the significance of ant-plant symbioses, the writer welcomed the opportunity of studying a somewhat similar species of this interesting genus. The results of the investigation are summarized in the following pages.

#### Taxonomy

One of the first difficulties encountered in studying a neotropical biocoenose, in which representatives of the higher plants, ants,



coccids, and other insects are closely associated, is the identification of the organisms concerned in the complex. Of course, the principle of significant figures must be considered in biology, as in physics and mathematics. The most detailed field observations and carefully planned experiments may lose much of their significance if an investigator fails to secure adequate information concerning the identity of the plants and animals with which he is working. In most cases, therefore, it is advisable to prepare museum specimens which may be preserved as a record for verification by other investigators. Typical herbarium specimens of all of the plants to be discussed in this and in subsequent papers have been deposited in the Gray Herbarium of Harvard University. Specimens of the insects have been preserved in the collections of Professor W. M. WHEELER, who collaborated with the writer in the investigation of the myrmecophytes of the Kartabo region. The ants were identified by him, the coccids by Mr. HAROLD MORRISON of the United States Bureau of Entomology, and certain parasitic Hymenoptera by Professor C. T. BRUES.

In dealing with *Cecropia*, one is concerned with a group of plants which present many taxonomic difficulties. The leaves of mature plants frequently are much too large for herbarium sheets of standard dimensions, and the inflorescences are difficult to season for museum purposes. Thus many of the descriptions of species are based upon the study of more or less fragmentary material. Furthermore, there appears to be as yet no consensus of opinion as to which of the foliar and floral characters are of the greatest diagnostic value. In view of these facts, the writer devoted considerable attention to the investigation of the variability of the morphological characters of the Kartabo species of *Cecropia*.

There proved to be two distinct species, a myrmecophytic species, with a well developed trichilium and numerous food bodies, and a non-myrmecophytic species, which is entirely devoid of these structures. The latter is considered by Dr. E. H. SNETHLAGE to be a variety (*decurrens*) of *C. sciadophylla* Mart. The former does not agree with any previously described species, and owing to its association with ants, was studied more intensively.



During the earlier juvenile stages the leaves of this species are small,  $\pm 6$  cm. long,  $\pm 2$  cm. wide, simple, lanceolate, finely serrate, pilose above and densely albido-tomentose below. The subsequently formed leaves increase rapidly in size, forming first three, then five, and ultimately nine to eleven lobes (text figs. 1, 2). As the juvenile leaves develop lobes, they lose their marginal serra-

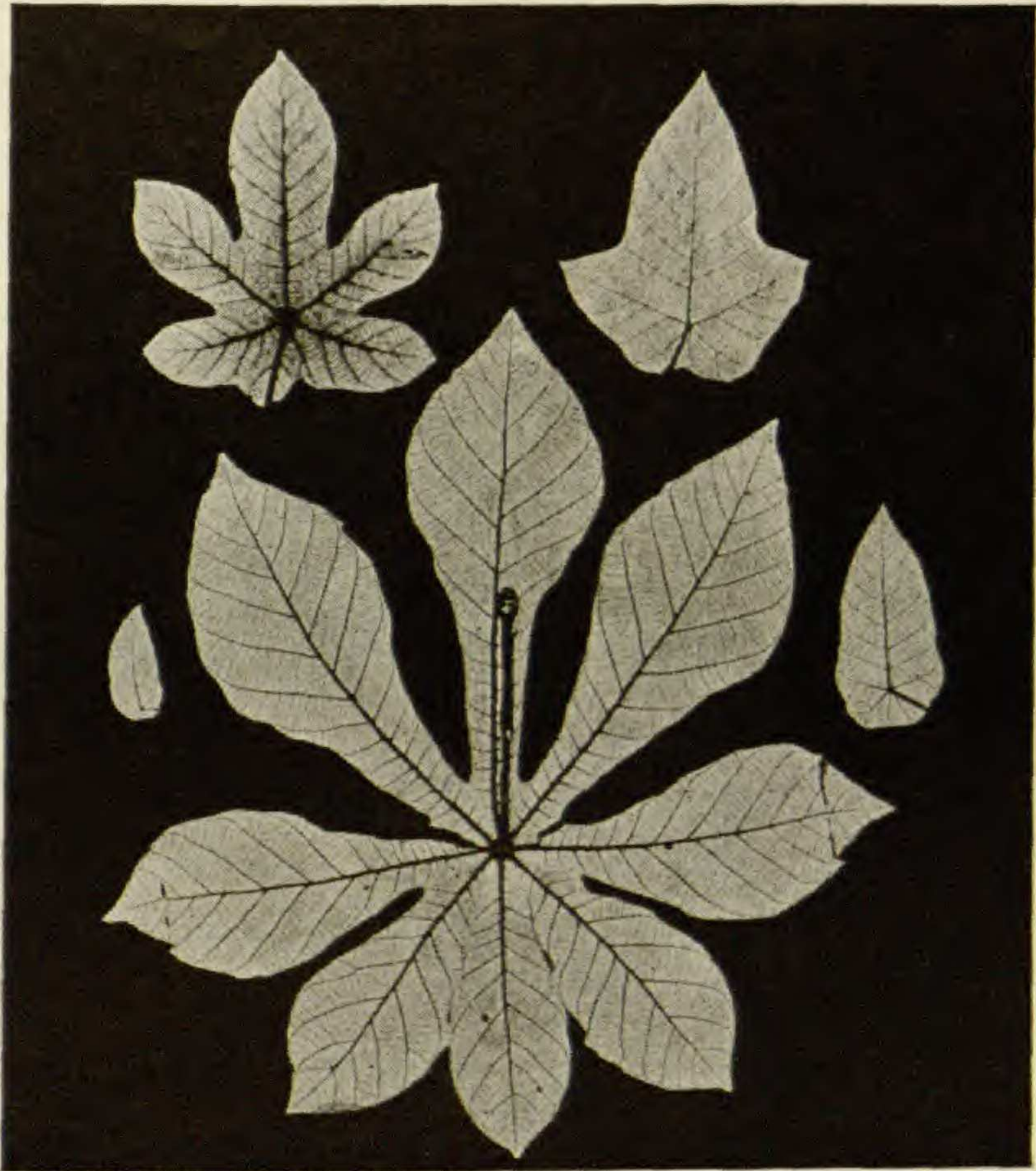


FIG. 1.—*Cecropia angulata*: leaves from juvenile plants of different ages, showing white tomentum and formation of lobed lamina;  $\times \frac{1}{5}$ .

tions and become sharply asperate upon the upper surface. The transitions from the juvenile to the typical adult foliage are gradual, and may be deferred until relatively late stages in the ontogeny of the plant. Thus the large deeply lobed leaves of tall saplings may retain many of the juvenile characters, that is, asperate upper surface, chartaceous texture, conspicuous white tomentum on the under surface, acuminate lobes, etc. The leaves of adult indi-



viduals are huge, 56-98 cm. long, 56-84 cm. wide, coriaceous, glossy glabrous above, and are provided with only a microscopic layer of closely appressed white hairs in the areoles of the lower

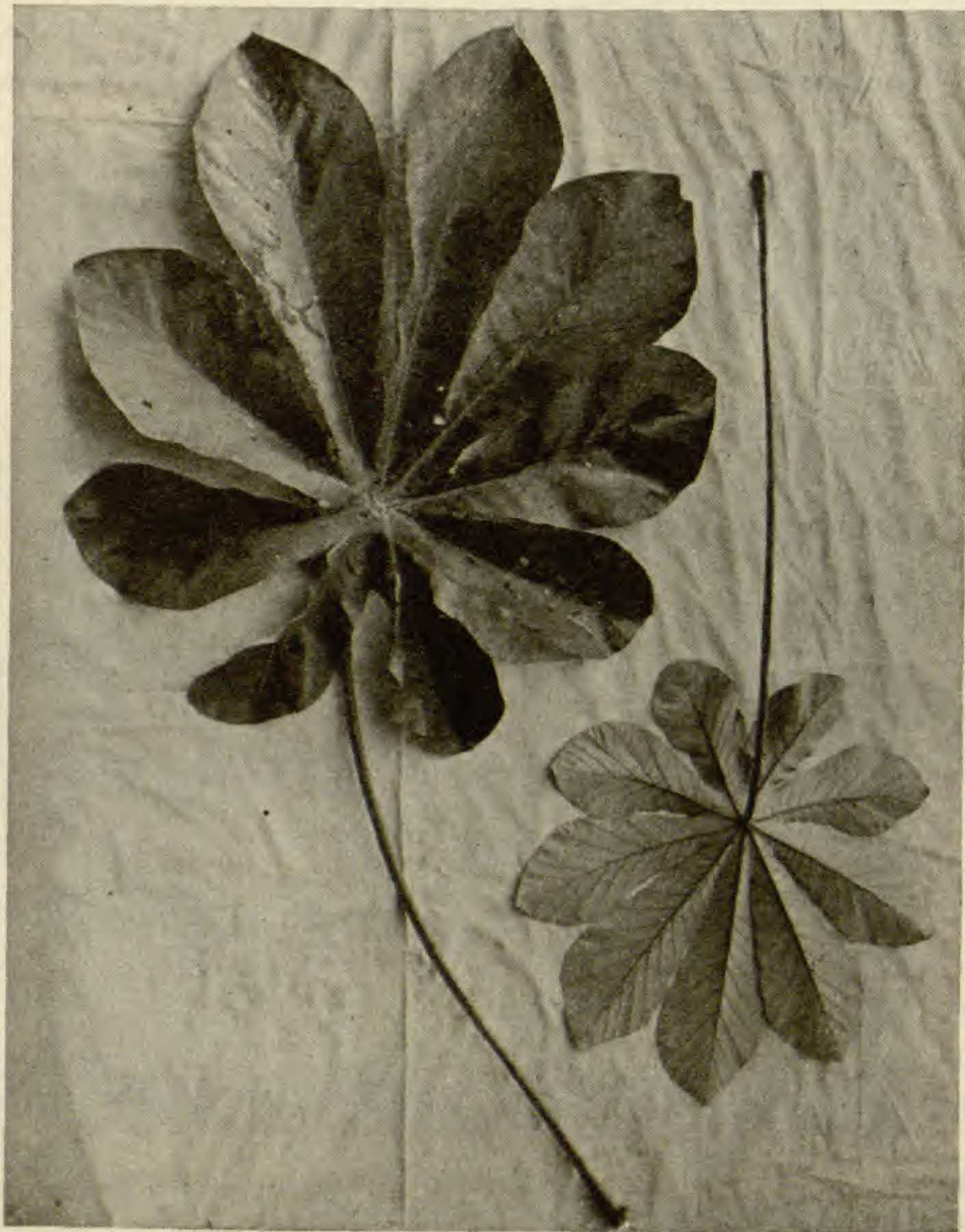


FIG. 2.—*Cecropia angulata*: typical leaves from tall tree, showing variability in size;  $\times \frac{1}{14}$ .—Photograph by JOHN TEE-VAN.

surface. They are divided to within 4-7 cm. of the base into 9-11 cuneate-obovate or spatulate lobes which have undulate margins (text fig. 2).

Although at first sight most of the vegetative characters appear to be extremely variable, many of them are relatively stable during



specific stages in the ontogeny of the plant. For example, the leaves of adult individuals always are deeply lobed and undulate on the margins, never scabrous on the upper surface or conspicuously

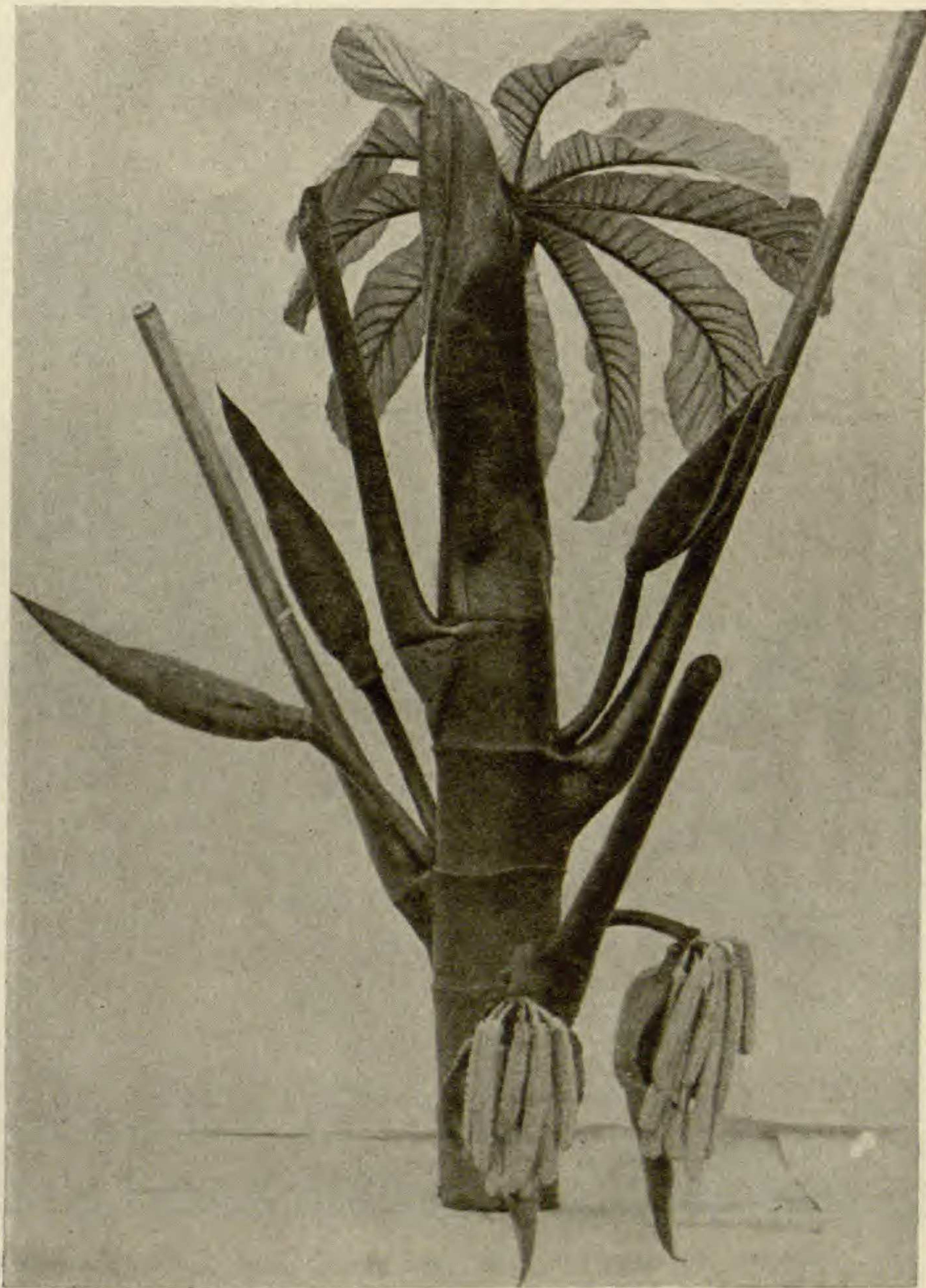


Fig. 3.—*Cecropia angulata*: terminal shoot of tall, vigorous young tree, showing ♂ inflorescences, and foliar and floral bracts;  $\times \frac{1}{10}$ .—Photograph by JOHN TEE-VAN.

tomentose below; whereas the leaves of juvenile plants always are hairy or sharply asperate above, and are densely albido-tomentose on the under surface. It is evident, therefore, that in distinguish-



ing species of *Cecropia* it is essential to compare leaves from plants of similar age classes, and, so far as possible, to avoid generalizations based upon highly variable, transitional types of foliage, such as occur on saplings.

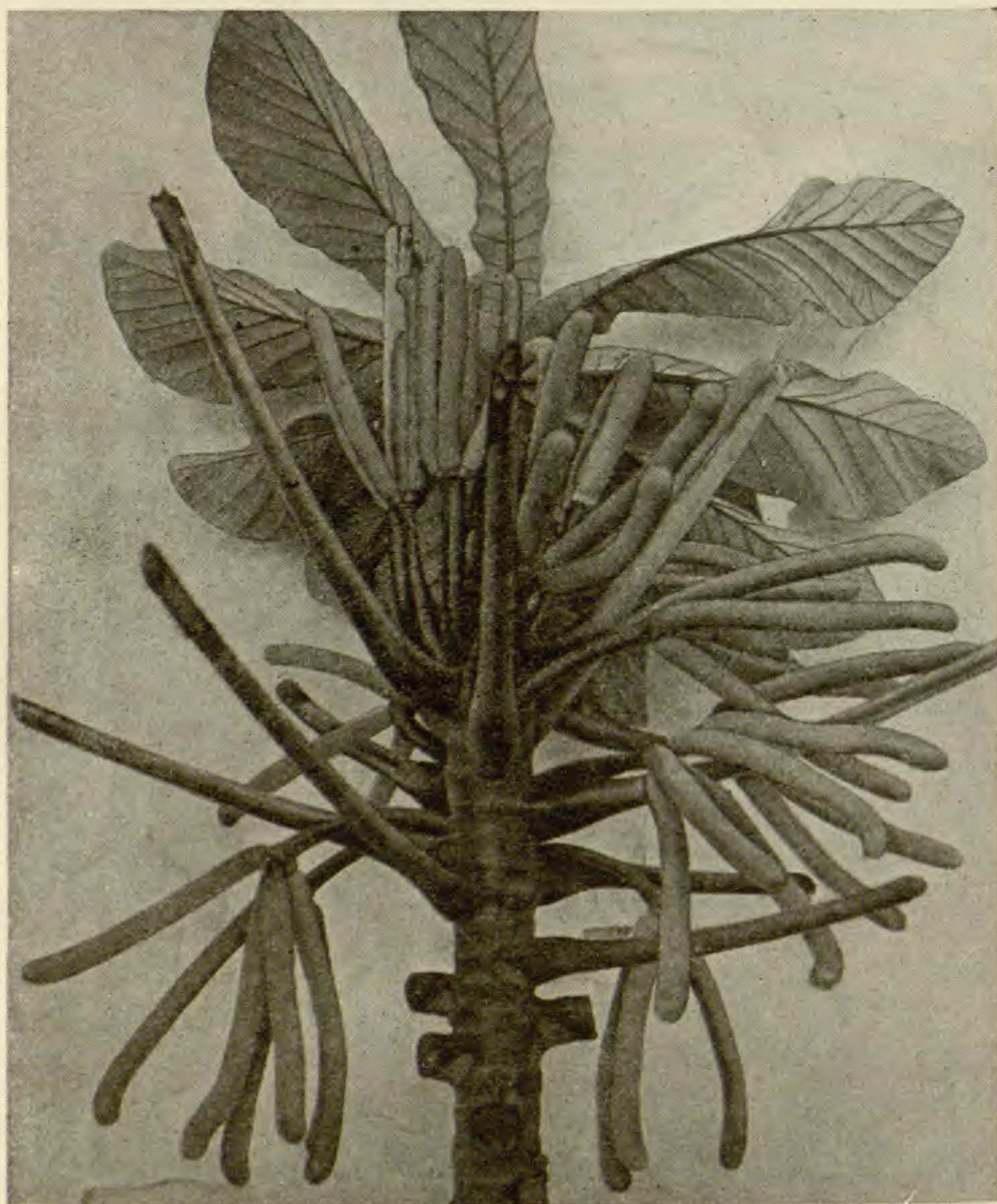


FIG. 4.—*Cecropia angulata*: terminal shoot of old, slow growing tree, showing ♀ aments in different stages of development;  $\times \frac{3}{18}$ .—Photograph by JOHN TEE-VAN.

Certain of the floral characters are variable, whereas others are relatively stable. The bracts which envelop the young inflorescences are coated during the later stages of their development with dense, rufous tomentum, and are frosted with long white hairs. The male and female aments (text figs. 3, 4) vary in size



during different stages of their ontogeny, but the former (text fig. 5A) retain their juvenile angularity, whereas the latter (text fig. 6D) become nearly cylindrical at maturity. The peduncles vary considerably in length, but are asperate in both sexes. The female inflorescences are characterized by having one or more perigones in the sutures between the short, stout, conferruminate

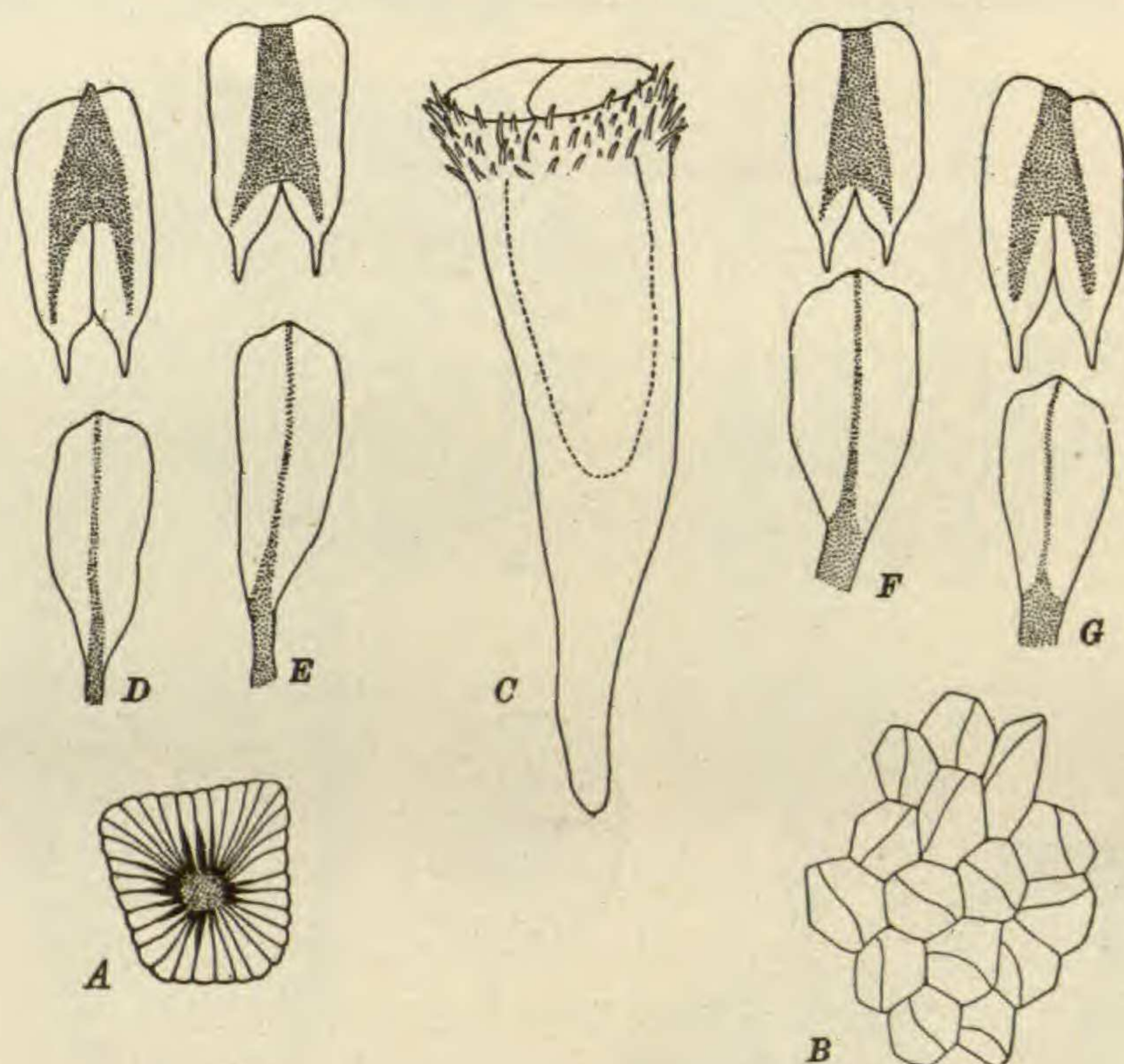


FIG. 5.—*Cecropia angulata*: A, cross-section of  $\delta$  ament,  $\times 2.5$ ; B, surface view of portion of  $\delta$  ament, showing pentangular and hexangular, apically cleft perigones,  $\times 10$ ; C,  $\delta$  perigone, showing collar of short, stiff hairs, and position of perigonial chamber,  $\times 22$ ; D, lower stamen of pair; E, upper stamen of same pair; F, upper stamen of pair from another perigone; G, lower stamen of this pair; (D-G)  $\times 22$ .

pedicels (text fig. 7C). The clavate, pentangular or hexangular, apically cleft male flowers are not jacketed by a dense mat of long, interlacing trichomes, but are provided with a collar of short, stiff hairs (text fig. 5). The perigonial chamber is confined to the upper half of the flower, and the caudate anthers are borne on short filaments which become extraordinarily broad and membranaceous at the time of dehiscence (text fig. 5). The filaments, connectives, and anthers vary considerably in size and shape (text fig. 5D-G);



for example, the upper anther of each pair tends to be somewhat smaller, and to be attached nearer its base to a longer filament. The connective may or may not project beyond the apex of the anther. The pentangular or hexangular perigones of the female aments (text fig. 6) are characterized by having three distinct types of trichomes. They are jacketed both internally and externally by dense mats of long, interlacing hairs (text fig. 7). In addi-

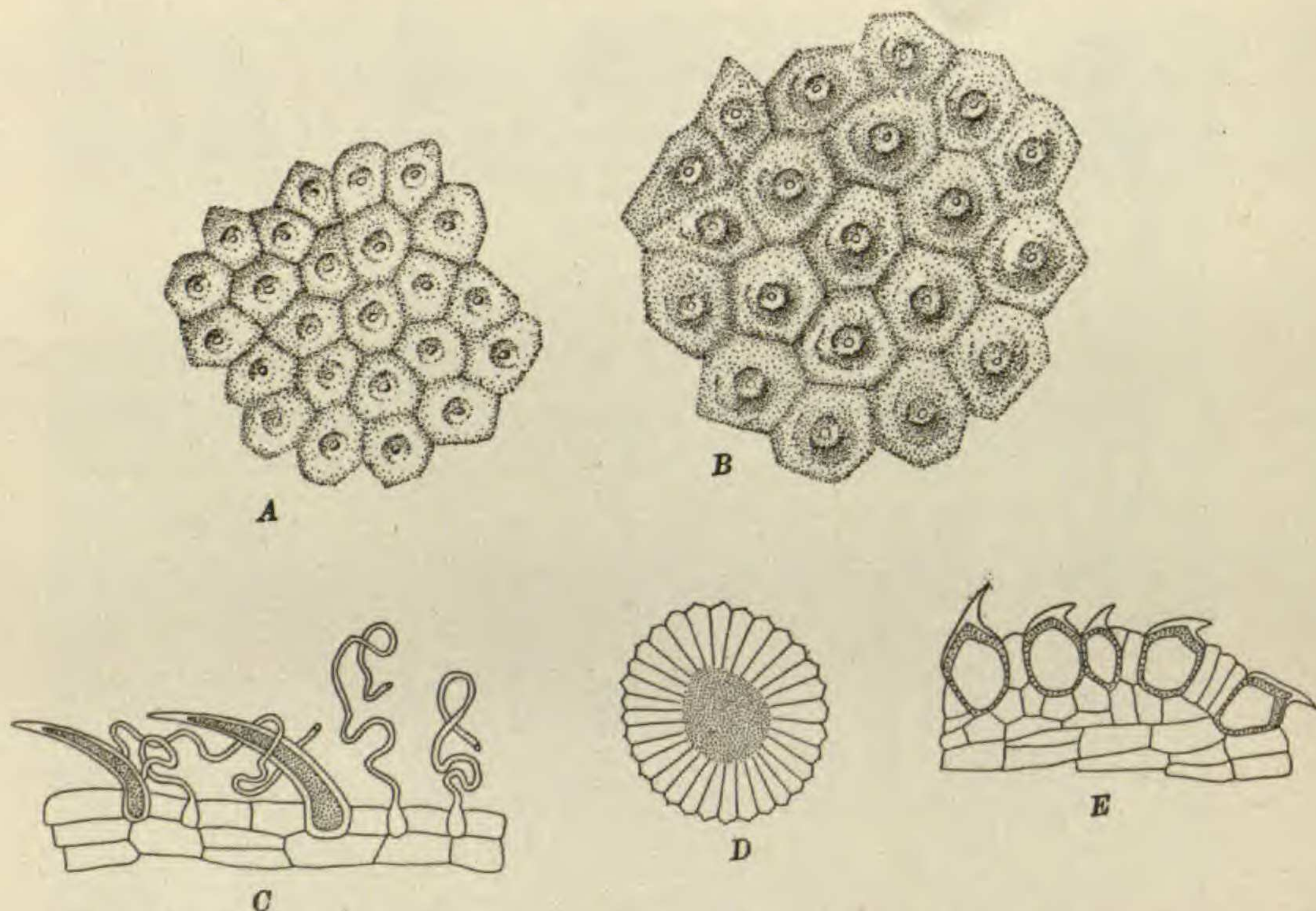


FIG. 6.—*Cecropia angulata*: A, surface view of portion of ♀ ament, showing pentangular and hexangular perigones at fertilization,  $\times 10$ ; B, surface view of portion of ♀ ament, showing enlargement of perigones during earlier stages in formation of seed,  $\times 10$ ; C, two types of trichomes from inner wall of perigone,  $\times 315$ ; D, cross-section of ♀ ament at fertilization,  $\times 2.5$ ; E, trichomes from outer apical portion of perigone (similar bristles occur on style);  $\times 315$ .

tion, they have a crown of extremely short, stout bristles on the margins of their exposed apical surface, and a fringe of longer bristles which project into the constricted upper portion of the perigonial chamber (text fig. 6). The glabrous, almond-shaped ovary is mottled, dark gray, and bears a cylindrical style which terminates in a comose stigma (text fig. 7). The style is provided with short, stout bristles, such as occur on the apical portion of the perigone. During the development of the seed, the perigone



enlarges and becomes somewhat modified in form and structure (text figs. 6, 7). The white tomentum is carried outward, so that the lower two-thirds of the flowers are not held together by inter-

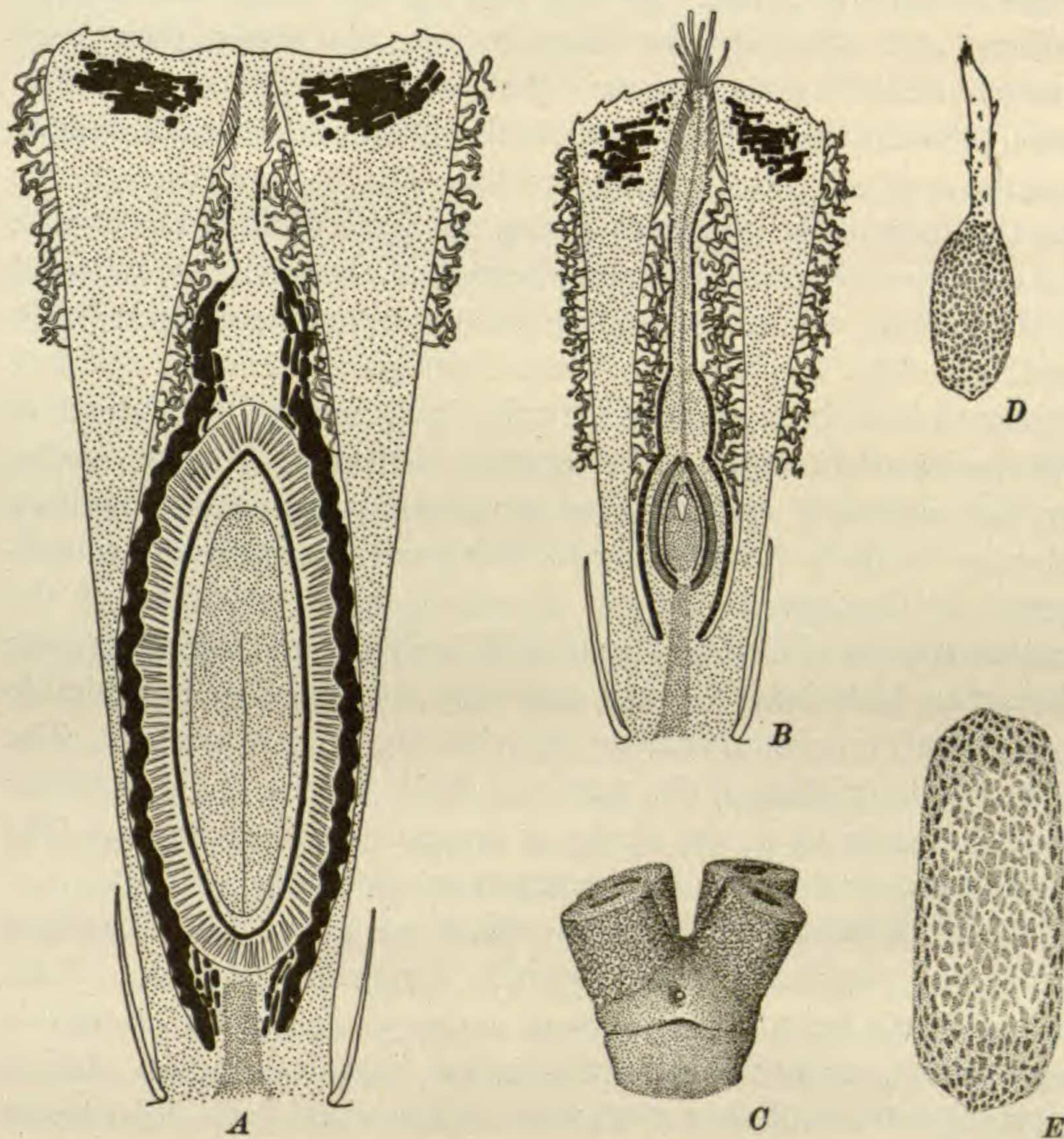


FIG. 7.—*Cecropia angulata*: A, longitudinal section of ♀ perigone and nearly mature seed, showing embryo and various seed coats,  $\times 31$ ; B, longitudinal section of ♀ perigone, style, ovary, and ovule, showing various types of trichomes,  $\times 31$ ; C, basal portion of ♀ inflorescence, showing perigone at point of contact of conferruminate pedicels,  $\times \frac{1}{10}$ ; D, ovary and style,  $\times 18$ ; E, mature seed,  $\times 20$ .

lacing hairs, and an annular depression is formed in the exposed outer surface of each perigone. At maturity the scurfy, dark reddish brown, oblong seeds (text fig. 7E) have a more or less symmetrical, lozenge-shaped, triangular or rectangular contour in cross-section.



Owing to the variability of many of the floral characters during the enlargement of the aments, there is a considerable element of uncertainty in comparing inflorescences which are not in equivalent stages of differentiation. In the case of the male aments, the anthers, and especially the filaments, do not attain their most characteristic size and shape until just before dehiscence. Furthermore, there are two distinct stages in the differentiation of the female aments, one before and one after fertilization. The changes in the size and form of the perigones during the maturation of the ovules, and subsequently during the enlargement of the seeds, are reflected in the aments, whose external characters become correspondingly modified. The significance of these developmental stages does not appear to have been appreciated fully by a number of students of the species of *Cecropia*. The aments, perigones, stamens, seeds, etc. are described and are used for diagnostic purposes without reference to their variability or to their particular stage of development. Until more is known concerning the variability of the various species of *Cecropia*, and until their more stable diagnostic characters have been isolated and fully described, it is desirable to give rather comprehensive descriptions of new species. The following description of the myrmecophytic species of the Kartabo region is based upon the study of typical adult specimens. The juvenile characters have been referred to previously.

***Cecropia angulata*, sp. nov.**—Arbor 10–25 m. altus, caulibus ramisque juvenibus argute asperatis formicosis (*Azteca*). Folia ampla rubella vel viridia 56–98 cm. longa 56–84 cm. lata profunde 9–11-lobata, lobis cuneato-obovatis vel spatulatis, apice obtusis vel rotundatis saepissime mucronatis, margine undulatis, lobo medio 36–60 cm. longo 13–24 cm. lato, nervis secundariis 15–20, lamina supra glabra nitente (post exsiccationem castanea obscurata) infra in nervis venis venulisque galbrata, in areolis solis tenuiter (microscopice) albido araneoso-tomentosa et in disco centrali breviter griseo-villosa, petiolo cylindrico (post exsiccationem costato) 50–120 cm. longo glabro vel albido-tomentoso ad basin incrassato et cum trichilio albido (tardius castaneo) instructo. Stipulae vaginantes maximae castaneae paullo griseo-tomentosae. Amentae ♂ 14–18 rectae rigidae *angulatae* 5–12 cm. longae 4–7 mm. crassae in



pedicellis tenuibus 5-17 mm. longis gestae et in spatha castanea griseo-tomentella fusiformi ad basin constricta 14-16 cm. longa inclusae. Amentae ♀ 4 rectae rigidae vel apice paullo curvatae cylindricae ante anthesin 9-12 cm. longae 7-8 mm. crassae (tardius 13-17 cm. longae 11-13 mm. diametro) in pedicellis crassis confer-ruminatis 3-7 mm. longis gestae et in spatha castanea griseo-tomentella quadrangulata obtusa 10-12 cm. longa inclusae. Ped-unculi argute asperati compresso-cylindrici, ♂ 9-12 cm. longi 8-11 mm. crassi, ♀ 8-10 cm. longi 7-10 mm. crassi. Perigonia ♂ clavata pentangularia vel hexangularia 2-3 mm. longa, filamentis in maturi-tate membranaceis 0.5-1.4 mm. longis 0.3-0.5 mm. latis, antheris caudatis 0.8-1.0 mm. longis 0.4-0.5 mm. latis. Perigonia ♀ pen-tangularia vel hexangularia cum albido tomento vestita ad anthesin 1.5-2.0 mm. longa deinde usque ad 3.0-3.5 mm. elongata. Stylus cylindricus ovarium aequans vel eo longior. Stigmata comosa. Fructus maturus furfurosus rubidus 2.0-2.5 mm. longus.

Kartabo region, British Guiana: *I. W. Bailey* (1920), nos. 3, 4, 5, 6, 8, 9, 14, 15, and 17; Kangaruma, British Guiana: *H. A. Gleason* (1921), no. 198.

The fistulose stems of *Cecropia angulata* are inhabited by four distinct species of *Azteca*; a majority of the plants are colonized by a black species, *A. constructor* Emery, a considerable number by a yellowish species, *A. alfaroi* Emery, and an occasional isolated individual by either *A. instabilis* F. Smith or *A. trigona* subsp. *mediops* Forel. The following observations upon the habits of the guest ants are based upon a study of the first two species.

Of the coccids which are associated with *Azteca*, *Pseudococcus rotundus* Morrison is the commonest species. *Akermes quinquepori* Newstead and *Pseudococcus bromeliae* Bouché are of more or less sporadic occurrence.

### Are Cecropias protected by their guest ants?

In studying the remarkable leaf cutting and fungus growing habits of the neotropical Attine ants, BELT (2) became much impressed by the efficiency of these insects in defoliating large numbers of native and introduced plants, and he was led to wonder how tropical vegetation has survived their devastating attacks. He inferred that the leaves of many plants are distasteful to the



ants or are unsuitable for their purposes, and that other plants are provided with special means of defense. He concluded that the so-called bull's-horn Acacias and other myrmecophytes are protected by their guest ants, which drive away their leaf cutting relatives. MÜLLER (6) and SCHIMPER (8) endeavored to prove that the myrmecophytic species of *Cecropia* are protected by the ants which inhabit their fistulose stems and branches. They found that plants which were colonized by Aztecas were not molested by Attine ants, whereas uninhabited individuals were more or less completely defoliated by them.

That BELT, MÜLLER, and SCHIMPER tend, on the one hand, to exaggerate the destructiveness of the leaf cutting ants, and on the other hand to overemphasize the protection afforded by the guest ants, has been suggested by VON IHERING (4), RETTIG (7), ULE (9), FIEBRIG (3), WHEELER (10), and other critics of the theory of myrmecophily. Several of these investigators call attention to the fact, previously noted by MÖLLER (5), that the leaf cutting ants feed upon a great variety of plants, and show no particular preference for the foliage of *Cecropia*. Thus, although the Attine ants frequently are troublesome pests in gardens and orchards, their feeding habits under normal conditions are such that they are not likely to exterminate indigenous species. According to VON IHERING's computations, 183 nests of leaf cutting ants consume no more foliage during a year than does a single cow. In many cases the myrmecophytes grow in regions, such as swamps and periodically inundated areas, where the fungus growing Attas do not occur. Furthermore, during the earlier stages of its development *Cecropia* is not inhabited or protected by its putative guardians. In addition, it has been shown that plants which are not inhabited by Aztecas may remain unmolested by Attas for long periods, and that trees which are inhabited may be seriously injured by phytophagous insects and sloths. Of course it must be admitted in this connection that the discrepancies between the conclusions of MÜLLER and SCHIMPER and those of ULE, VON IHERING, and others, may be due to the fact that they were concerned with different species of Attine ants. Furthermore, it may be argued that the juvenile



plants do not need the protection of the Aztecas, since they are immunized by various protective devices.

In the forests of the Kartabo region there are numerous colonies of the common leaf cutting and fungus growing ant, *Atta cephalotes* L. The writer found, as MÖLLER had previously done in the case of *A. discigera* Mayr., *A. hystrix* Latr., and *A. coronata* Fabr., that this ant utilizes the leaves of a great variety of plants in the construction of its fungus gardens. In virgin and second growth forests, it seldom works for any considerable length of time upon a particular type of plant, but continually shifts its activities from one species to another. Owing to this fact and to the rapid recovery from injury by plants in moist tropical environments, the effects of its attacks upon a given species appear to be more or less evanescent. Its normal leaf cutting habits, however, may be considerably modified under unusual or abnormal conditions. It frequently exhibits a strong preference for plants to which it has not previously been accustomed. Thus its attacks upon certain exotic plants in gardens and orchards at times may prove to be singularly persistent and destructive.

In many cases *Cecropia angulata* is not colonized by its guest ants until it has attained a considerable size. This is largely due to the fact that the young, fecundated queens, which initiate the new colonies, are killed by a Hymenopterous parasite, *Conoaxima aztecicida* Brues. Such plants are no more subject to defoliation than are the inhabited individuals. In order to determine whether the leaves of the juvenile *Cecropia* are distasteful to the leaf cutting ants, or are unsuitable for their purposes, a number of young plants were placed in close proximity to a large nest of *Atta cephalotes*. Leaves of adult *Cecropias* and of various other plants were used as controls. Although the ants worked upon this material in a more or less sporadic fashion, and showed a strong preference for certain types of leaves, they devoted no more attention to the mature than to the juvenile foliage of *Cecropia angulata*. In view of the fact that both BELT and SCHIMPER admit having seen young myrmecophytes defoliated by *Attas*, there appears to be little evidence in favor of the suggestion that juvenile ant-plants are less suscept-



ible to the attacks of phytophagous insects than are the adult individuals.

In defending the theory of myrmecophily, SCHIMPER placed great emphasis upon the discovery, in the Corcovado near Rio de Janeiro, of a species of *Cecropia* which is devoid not only of ants, but also of prostomata and Müllerian food bodies. He inferred that this *Cecropia* possesses no adaptations for attracting a defending army of Aztecas, because it is protected by a waxy coating which prevents the leaf cutting ants from climbing its stems. *Cecropia sciadophylla* Mart. var. *decurrrens* Snethlage is not colonized by Aztecas, but, as will be shown later, is provided with conspicuous and highly differentiated prostomata. The external surfaces of the plant are scabrous and afford a firm foothold for ants, as evidenced by the fact that several species of these insects were seen climbing its stems and branches. This species of *Cecropia* is no more subject to defoliation by *Attas* than is *Cecropia angulata*. That the leaves may be utilized in the construction of fungus gardens is shown by the fact that, when cuttings from plants of various ages are placed near nests of *Atta cephalotes*, the ants frequently transport a portion of the foliage into their subterranean dwellings.

SCHIMPER'S critics place considerable emphasis upon the fact that the myrmecophytic *Cecropias* may be inhabited simultaneously by two or more distinct genera of ants. To infer from this, however, that the Aztecas are indifferent to the presence of other ants is somewhat misleading. Although species of *Cecropia* were found that were inhabited by *Cryptocerus*, *Crematogaster*, stingless bees, etc., these insects were always confined to the older and lower internodes, which had been abandoned by the Aztecas. In spite of this marked segregation of the colonies in different levels of the stem, fierce conflicts may be waged for possession of the intervening internodes. Thus, the internodal cavities, where the colonies come in contact, frequently are filled with the corpses of dead warriors. The Aztecas are dominant, and in general do not tolerate the presence of other ants, in those portions of the stems and branches which are provided with leaves and food bodies. SCHIMPER found that when leaf cutting ants were deposited upon the terminal portions of a *Cecropia*, they were quickly seized by the Aztecas, if



their presence was discovered, and were hurled to the ground. How then may one account for the defoliation of trees which are inhabited by Aztecas? When a *Cecropia* is touched or shaken, the angry and aggressive Aztecas rush out of their nests and swarm over the whole plant, but under normal conditions only a limited number of workers are visible on the stems and bases of the petioles. Furthermore, there are periods during which the entire colony is quiescent, that is, has withdrawn into its nest. It is well known that these periods of quiescence are not the same in the case of different species of ants. Thus, certain ants are nocturnal, others are active at temperatures when other species are inactive, etc. In other words, as suggested by MÜLLER and MÖLLER, a *Cecropia* may be defoliated by leaf cutting ants during periods when the Aztecas are quiescent.

### Prostomata

Above the insertion of every leaf in *Cecropia adenopus* there is a shallow groove, which terminates just below the next node in a roundish depression (text fig. 8). As the external depression corresponds to an internal one, the wall of the fistulose stem is very thin at this place, and is a mere diaphragm in a tube. SCHIMPER showed that this diaphragm is devoid of hard and tough elements (fibrovascular bundles, collenchyma, lignified parenchyma, etc.), such as occur in the adjoining portions of the stem. He inferred from this that the diaphragm originated as an adaptation for facilitating the entrance of ants. At the phylogenetic commencement of symbiosis, the ants bored an entrance through the groove, evidently because the wall of the stem was somewhat thinner there. In accordance with a custom that is almost invariably followed and is connected with the domestic arrangements in their nests, they tended to penetrate into the internodal cavity at its upper extremity (at the apex of the groove). All features which facilitated their entrance at this place were retained in the struggle for existence, and were accentuated through natural selection. This led eventually to the differentiation of a thin, weak diaphragm or prostoma (VON IHERING). In other words, although SCHIMPER admitted that the groove is due to the pressure of the axillary



bud, he maintained that its terminal portion is a highly specialized adaptation, acquired through the action of natural selection. On the contrary, RETTIG and FIEBRIG assert that the prostoma is merely the youngest or less highly differentiated portion of the groove, and that it is produced by the pressure of the axillary bud and other growth phenomena in the elongating internodes. The former investigator is of the opinion that the ants are deterred from excavating in the lower portion of the groove, not by mechanical obstructions, but by the occurrence of "laticiferous vessels" which are absent in the prostoma. It is to be emphasized in this connection, however, that RETTIG's and FIEBRIG's statements do not necessarily invalidate SCHIMPER's conclusion that the diaphragm is an adaptation which originated as a modification of a previously existing structure.

Under most growth conditions *Cecropia angulata* does not form a shallow groove which terminates in a conspicuous circular pit (text fig. 8). The more or less fusiform depression or rill is somewhat deeper in the upper than in the lower portions of the internode, but the differentiation of specialized or mechanical types of tissue is retarded throughout its extension (fig. 1). As the walls of the internode increase in thickness, after the initiation of secondary growth, this fusiform diaphragm of delicate parenchyma is slowly reenforced by tougher and denser tissues (fig. 3). The metamorphosis begins at the base of the groove, and gradually extends upward, but the ants excavate their exits before these changes have progressed very far. It is evident, therefore, that in the case of the myrmecophytic *C. angulata*, the whole groove is a potential prostoma. The exact location of the aperture is determined, not by the presence or absence of resistant tissues or of "latex" vessels, but by the relative thickness of different portions of the diaphragm. That the whole groove is a potential prostoma, and that the ants merely excavate their exits and entrances in its thinnest and most easily perforable portion, are indicated by the behavior of young queens in juvenile plants. In many instances, several queens attempt to occupy the same internode, and as many as five entrances were found cut at different levels of a single groove. Not only do the queens cut through the basal portions of the diaphragms under such conditions, but they may even excavate



entrances in portions of the internodes which are not provided with preformed depressions.

It may be argued that in *C. angulata* the whole groove has been modified as an adaptation to ants. Such an assumption is not warranted, however, when important facts in the anatomy of the non-myrmecophytic *C. sciadophylla* var. *decurrens* are taken into consideration. Although this species is not inhabited by Aztecas, it is provided with more tenuous and highly specialized diaphragms than is *C. angulata* (text fig. 8; fig. 2). The internodal groove is very

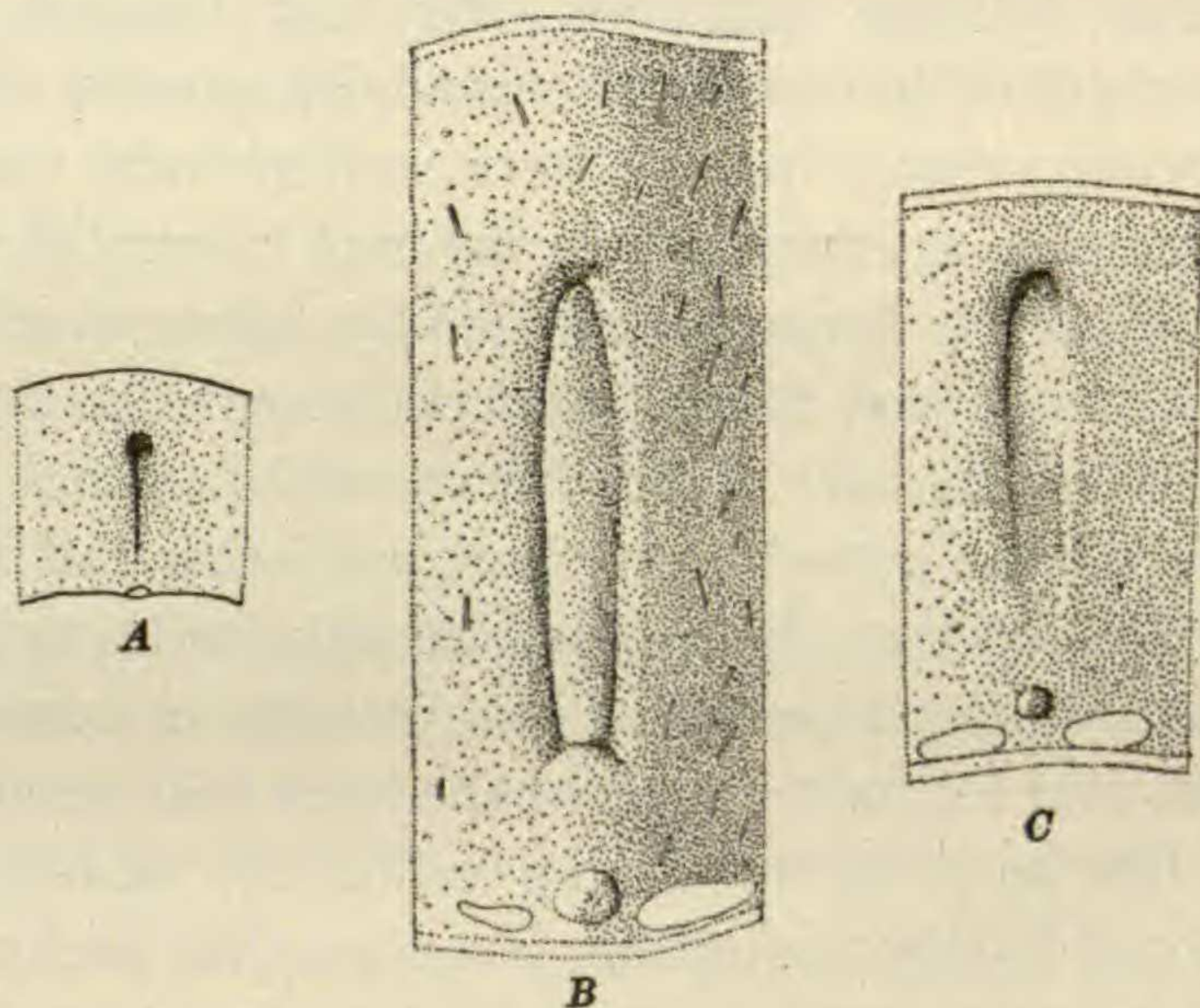


FIG. 8.—Prostomata or internodal diaphragms of various species of *Cecropia*: A, *C. adenopus*, after SCHIMPER; B, *C. sciadophylla* var. *decurrens*; C, *C. angulata*;  $\times \frac{1}{2}$ .

broad and deep, and the diaphragm, which is entirely devoid of tough tissues and secretory vessels, is composed of extremely thin layers of delicate parenchyma. Such facts as these suggest that the so-called prostoma of *C. adenopus*, and of other myrmecophytic species of *Cecropia*, is not an adaptation for attracting ants, but is merely a structural peculiarity, produced by the pressure of the axillary bud, which is utilized by the ants in their parasitism upon the plants.

### Feeding habits of guest ants

The *Azteca* colonies are initiated by young fecundated queens which cut entrances into the fistulose stems of juvenile plants. Although I examined hundreds of plantlets of *C. angulata*, none



of any considerable size were found that had been entered by but a single queen. The queens are so numerous that many of the successive internodes become inhabited, and, as already stated, one not infrequently finds that several queens have penetrated into the same internodal cavity. So far as it was possible to determine, however, a large proportion of these queens perish before they have produced a brood. A very considerable number are killed by the parasitic *Conoaxima aztecicida*, others are killed by their rivals in conflicts for possession of a given internode, and, as soon as the workers become numerous, they cut through the nodal partitions and kill all but one of the surviving queens.

When a young *Azteca* queen enters an internodal chamber, she covers the entrance aperture with a layer of triturated pith. The entrance subsequently becomes occluded by callus, which continues to grow internally, and finally projects some distance into the medullary cavity (fig. 4). Thus the queen is sealed within the internode during the period when she is initiating the new colony. In view of the fact that the queen is unable to leave her nest in search of food during a period of two months or more, MÜLLER, VON IHERING, and FIEBRIG infer that she must feed upon medullary tissue and the inwardly projecting callus or "stomatome." It should be noted in this connection, however, that such an assumption is based upon two more or less fallacious premises: (1) that the queen must feed during her period of isolation, and (2) that tissues which are gnawed or excavated by ants actually are eaten by them. Most students of the Formicidae are familiar with the fact that female ants are able to do without food, except such as is stored in their own bodies, for the greater part of a year, while they are founding their colonies. Furthermore, it is well known that many ants tend to gnaw into and smooth the walls of their nests, regardless of whether they are composed of living tissues or of inert materials. I was unable to find any evidence that the *Azteca* queens feed upon the tissues in the young internodes of *C. angulata*. The so-called stomatomes, upon which MÜLLER and VON IHERING place so much emphasis, are not uncovered and cut back by the queens until just before the first workers are ready to emerge from the nest, nor do they excavate the medullary tissue to any consider-



able extent, except when in search of material with which to block up the newly formed entrance aperture. Although VON IHERING is of the opinion that the luxuriant growth of callus is due to the stimulus of some substance excreted by the queens, I found that homologous structures may be produced by purely mechanical injuries.

With the advent of the first workers, the entrance to the primordial chamber is reopened, and the young colony either migrates to a higher internode or cuts through the nodal partitions into adjoining cavities. VON IHERING states that the Aztecas always abandon the primordial chamber and never perforate its upper and lower walls. Such is not invariably the case in *C. angulata*, for primordial chambers were frequently found in direct communication with internodes which were not provided with prostomal openings. Regardless of its exact mode of origin, the permanent domatium soon becomes stocked with food bodies by the young workers. These small beadlike structures (fig. 6), which are packed with fat and protein, are formed in large numbers in a curious cushion or mat of hairs, situated at the base of each petiole. The ripe food bodies are so assiduously collected by the ants that it is almost impossible to find one *in situ*, except in young uninhabited plants. Indeed, the ants frequently trim away the surrounding hairs and dig out the immature food bodies. SCHIMPER interpreted these so-called Müllerian corpuscles, and similar structures which occur on the leaflets of certain myrmecophytic species of *Acacia*, as metamorphosed glands or highly specialized allurements for attracting ants. RETTIG and others, however, have called attention to the fact that such glands occur on plants that are not frequented by ants, and it is difficult for the adherents of myrmecophily to account for such occurrences without resorting to the purely gratuitous assumption that they are survivals from former symbioses. ULE is of the opinion, in addition, that the expenditure of carbohydrates and nitrogenous substances, contained in these corpuscles, is not compensated for by the protection which the ants afford to the plants.

Although most investigators agree that the food bodies are an important item of food in the diet of the Aztecas, it has been



suggested that there are other potential sources of food in *Cecropia*. Thus, VON IHERING and FIEBRIG maintain that the imagines feed upon the succulent medullary tissues in immature internodes. It is true that the ants cut away the softer portions of the pith down to a hard, smooth peripheral layer of medullary tissue, but I found no evidence to indicate that this is not purely a process of house cleaning, such as occurs in many ant nests. In the moist, warm interiors of plants, ants have to contend with luxuriant growths of fungi which obstruct the cavities and interfere with the brood, unless they are held in check. The ants trim away the hyphae and cut back the substratum upon which these organisms tend to grow. FIEBRIG records having seen Aztecas busily engaged in excavating the pith, and in casting fragments of medullary tissue from their entrances, but such observations cannot be interpreted as evidence that the ants actually feed upon the tissues that they are removing.

Most students of the myrmecophytic species of *Cecropia* have found coccids associated with the ants which inhabit the fistulose stems. Their presence has been variously interpreted. BELT, MÜLLER, and ULE consider that they are tended by the ants which feed on their sugary exudations, but FIEBRIG states that the insects "in keinen direkten Verhältnis zu diesen Ameisen stehen." Having found a very close and significant relation between ants and coccids in most Ethiopian ant-plants, I devoted particular attention to the investigation of their behavior in *C. angulata*. I did not succeed in finding a single large, ant-inhabited specimen which did not contain numerous coccids. When a tree is split open the ants are as solicitous for the welfare of the coccids as they are for that of their eggs, larvae, and pupae. They seize them in their mandibles and carry them about until some unopened portion of the plant is found where they may be deposited in safety. In artificial nests, the workers spend hours in tending and stroking the coccids, and in feeding upon their sugary exudates. In view of these facts, it cannot be doubted that the miniature milch cows are an important source of liquid carbohydrates for the ants.

As in many of the African myrmecophytes, the ants excavate pits in the walls of their domatia which enable the coccids to reach



and feed upon the softer tissues of the *Cecropia*. Such excavations are essential, owing to the fact that the internodal, medullary cavity is entirely jacketed by a dense, horny layer of sclerenchyma. In the African ant-plants, the ants cut through to the cambium and induce the formation of a nutritive callus. In *C. angulata* the pits are not located in the sides of the internodal chamber, but in the nodal diaphragms. At the time when the ants begin their excavations, the nodal partition consists of five distinct layers (figs. 5, 7). The soft, internal layer, which is provided with strands of conducting tissue and which is fed upon by the coccids, is separated from the external layers of porous, medullary tissue by two layers of dense, thick walled tissue. The ants remove the two external layers and cut circular pits in the underlying sheets of horny sclerenchyma (figs. 8, 9). The coccids sit in these pits and thrust their setae into the succulent tissue which is thus exposed. That the pits are not made by the coccids, as suggested by VON IHERING, is indicated, not only by the fact the delicate sucking mouth parts of these insects are not adapted for excavating in dense tissues, but also by the fact that I have actually observed the ants in the process of excavating them.

### Summary and conclusions

The theory of myrmecophily, as modified by SCHIMPER, interprets the structural peculiarities of myrmecophytic species of *Cecropia* as adaptations for enlisting the services of an aggressive army of Aztecas which protect their hosts against the attacks of the leaf cutting Attine ants. Cleverly conceived and suggestive as this Neo-Darwinian hypothesis undoubtedly is, it appears to be based upon a series of plausible deductions or teleological inferences, and is open to serious criticism. The distribution and feeding habits of the Attine ants in luxuriant, tropical forests are such that the ants are not likely to exterminate indigenous species. They show no strong preference for the foliage of *Cecropia*, and rarely attack either inhabited or uninhabited trees. Although Aztecas tend to prevent other ants from visiting the terminal portions of the adult *Cecropias*, they do not protect the juvenile individuals. That the curious prostomata and Müllerian corpuscles



of *Cecropia adenopus* and of other myrmecophytic species of *Cecropia* are not allurements, acquired through natural selection, is indicated by the fact that such structures occur on certain species of *Cecropia* and other plants which are not frequented by ants. The *Azteca-Cecropia* associations, and ant-plants in general, are extremely interesting cases of parasitism, which illustrate the remarkable adaptiveness of ants in availing themselves of the potentialities of given environments. This is shown, not only in the utilization of the preformed food bodies, prostomata, and internodal cavities, but more strikingly in the structural modifications produced within the plants for the growth and tending of coccids. Thus, the ants are able to obtain food from the plant in two ways, fats and proteins directly from the Müllerian corpuscles, and carbohydrates vicariously through the coccids.

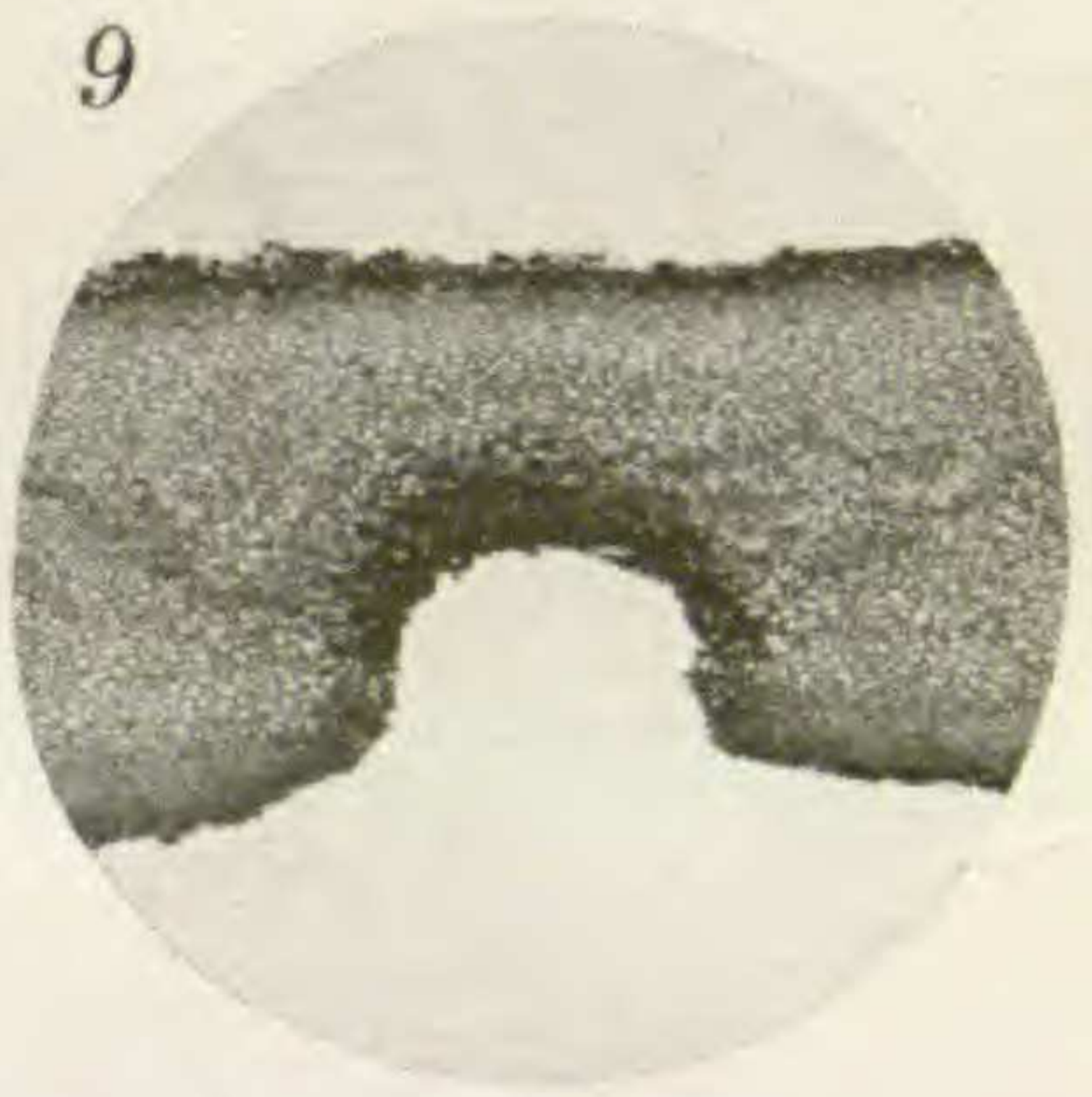
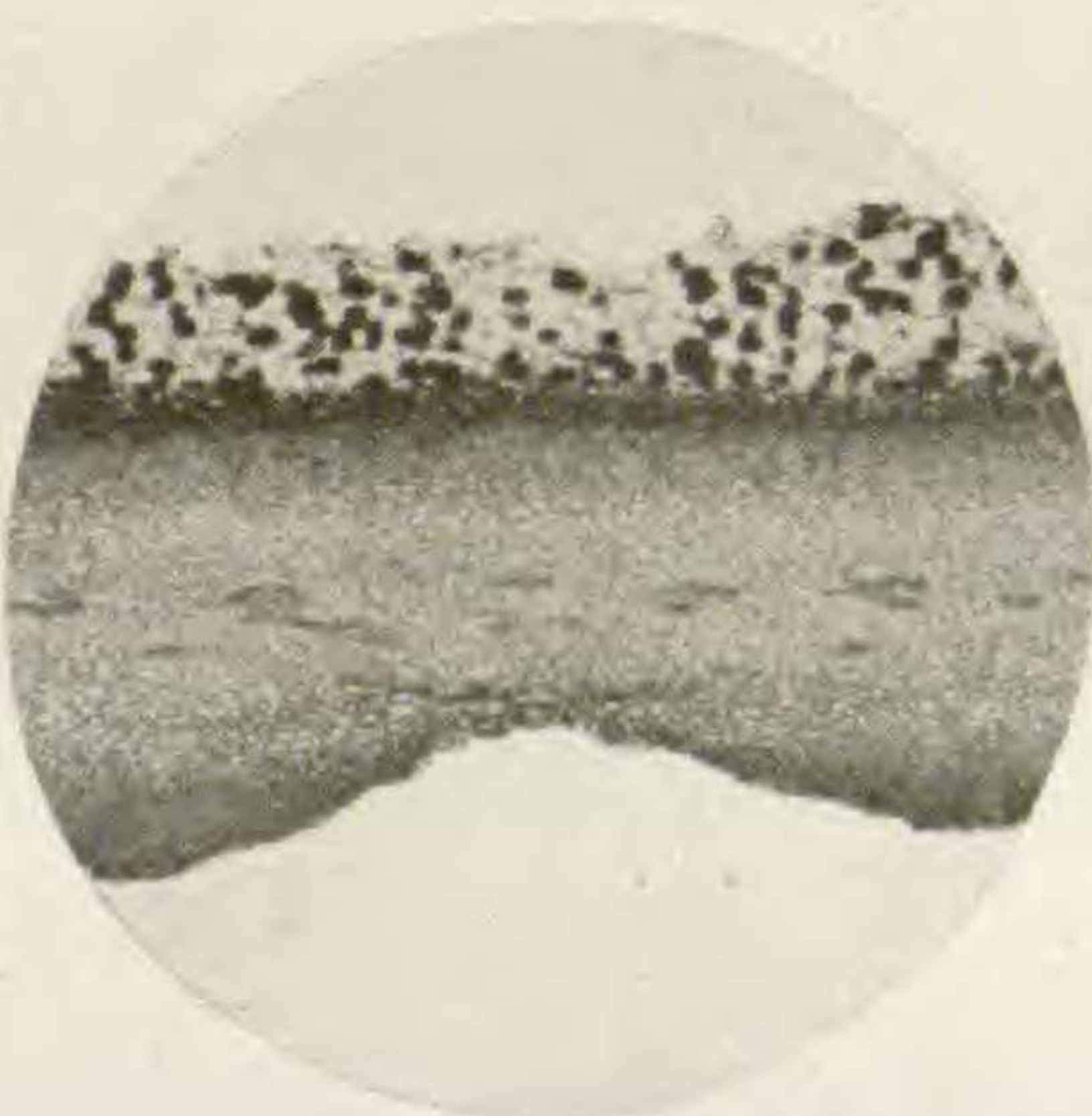
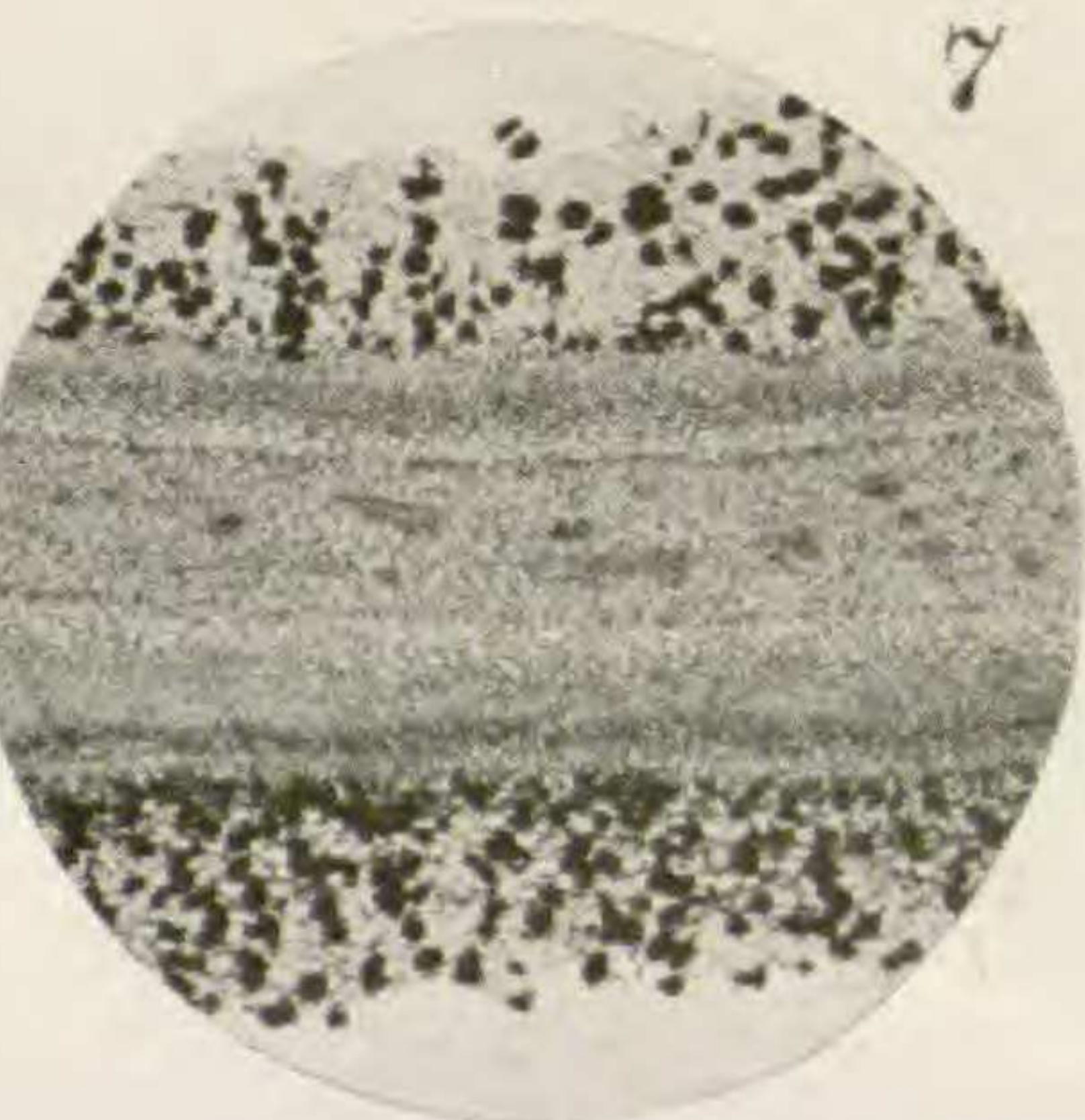
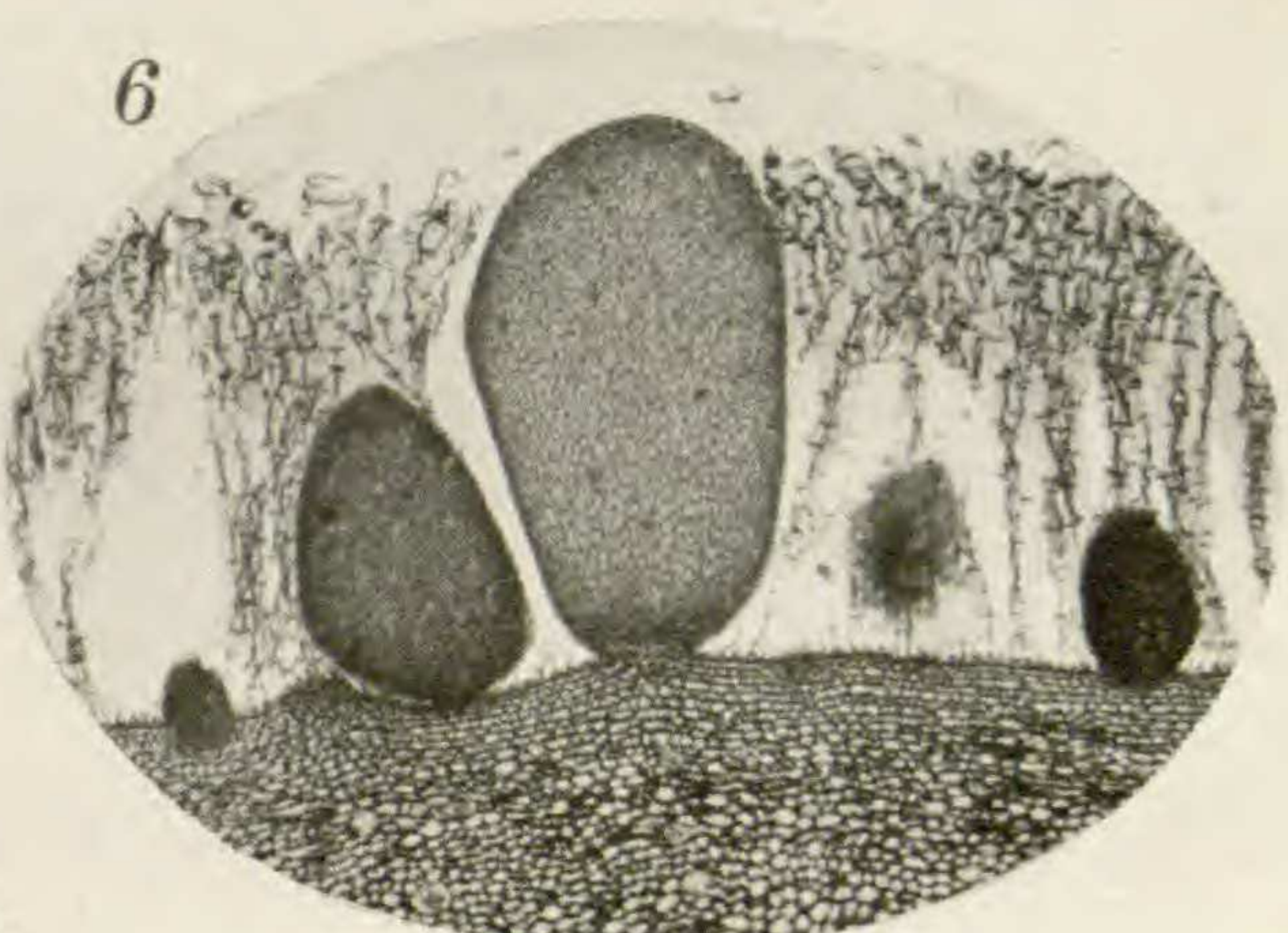
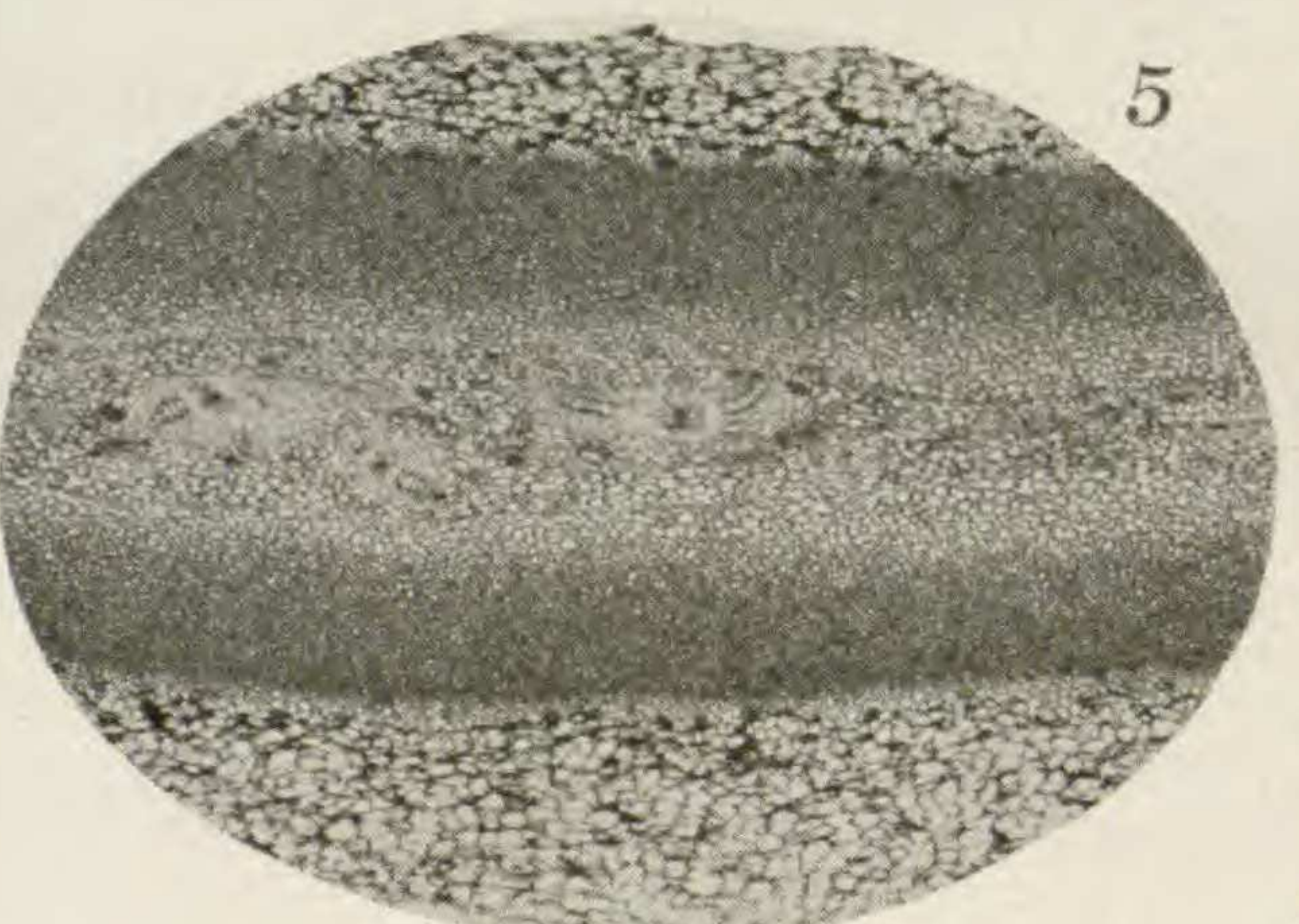
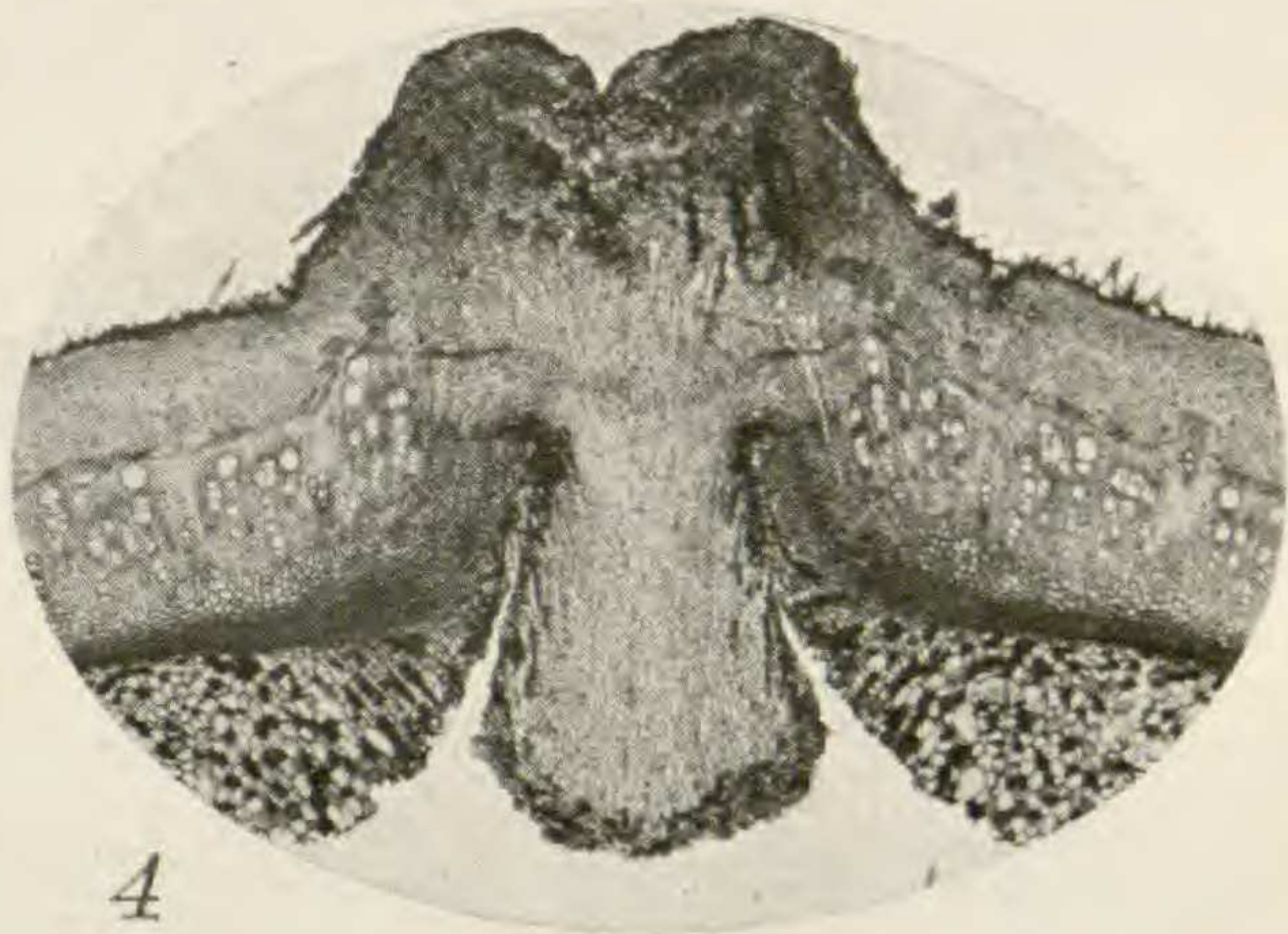
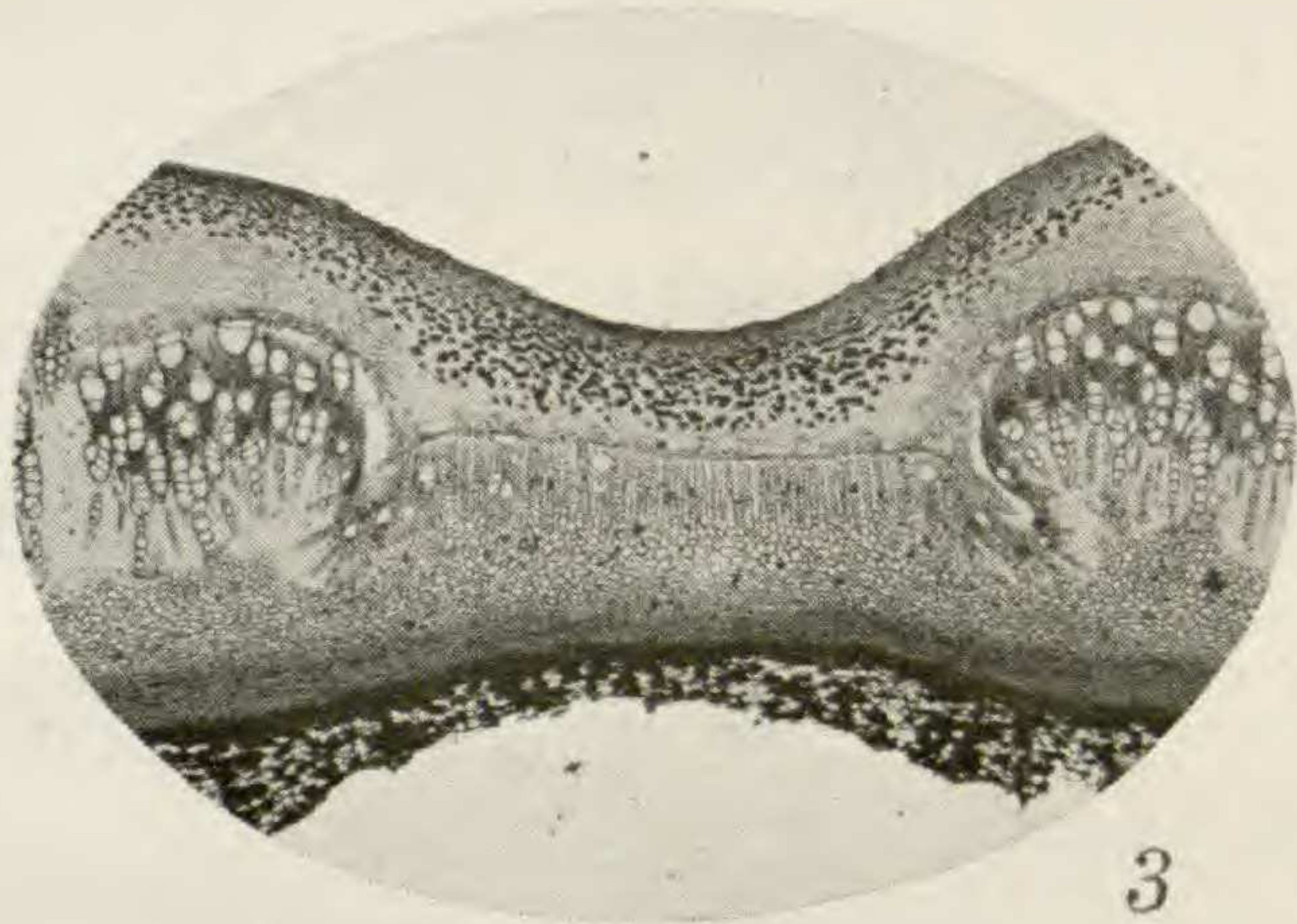
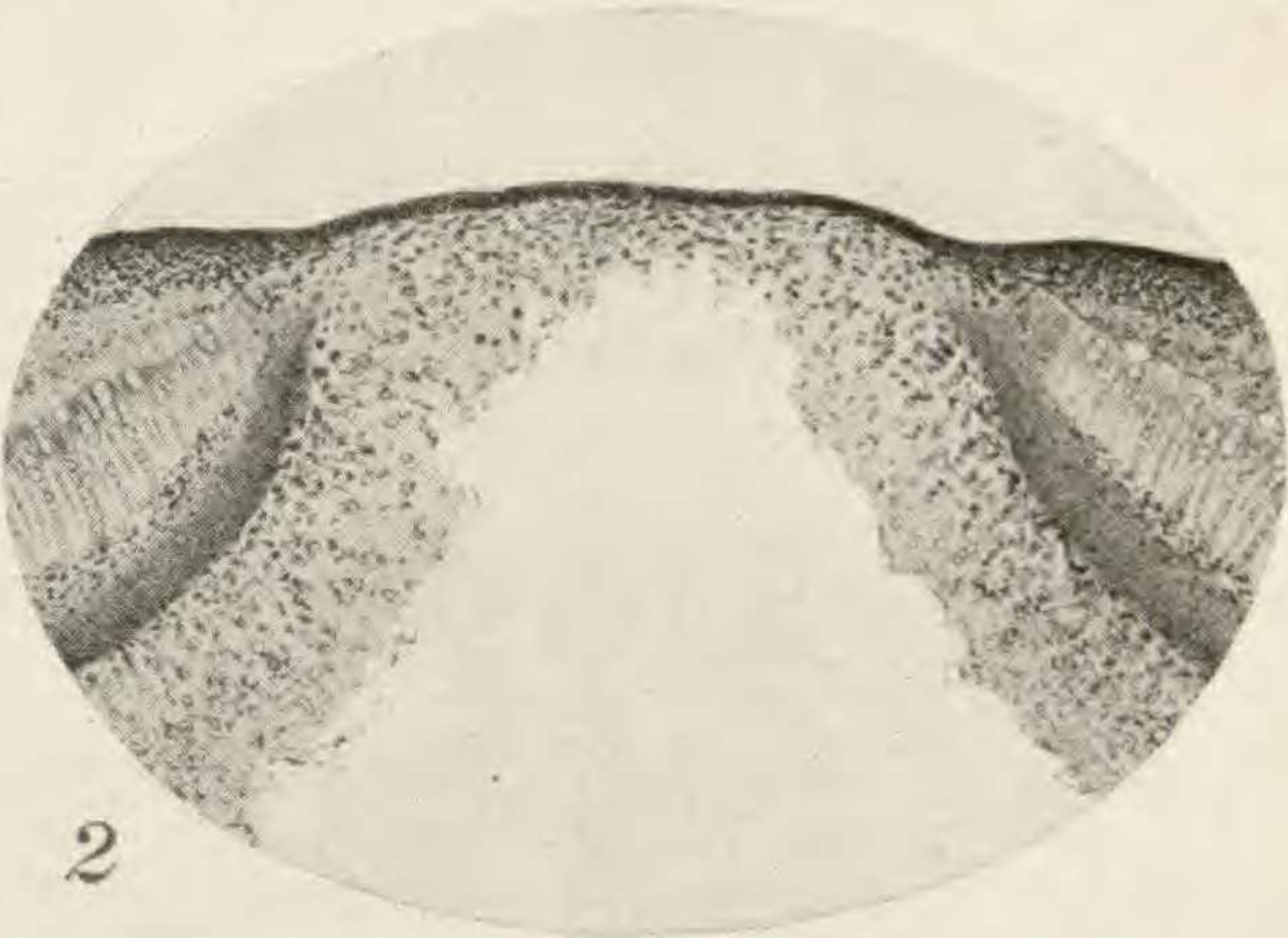
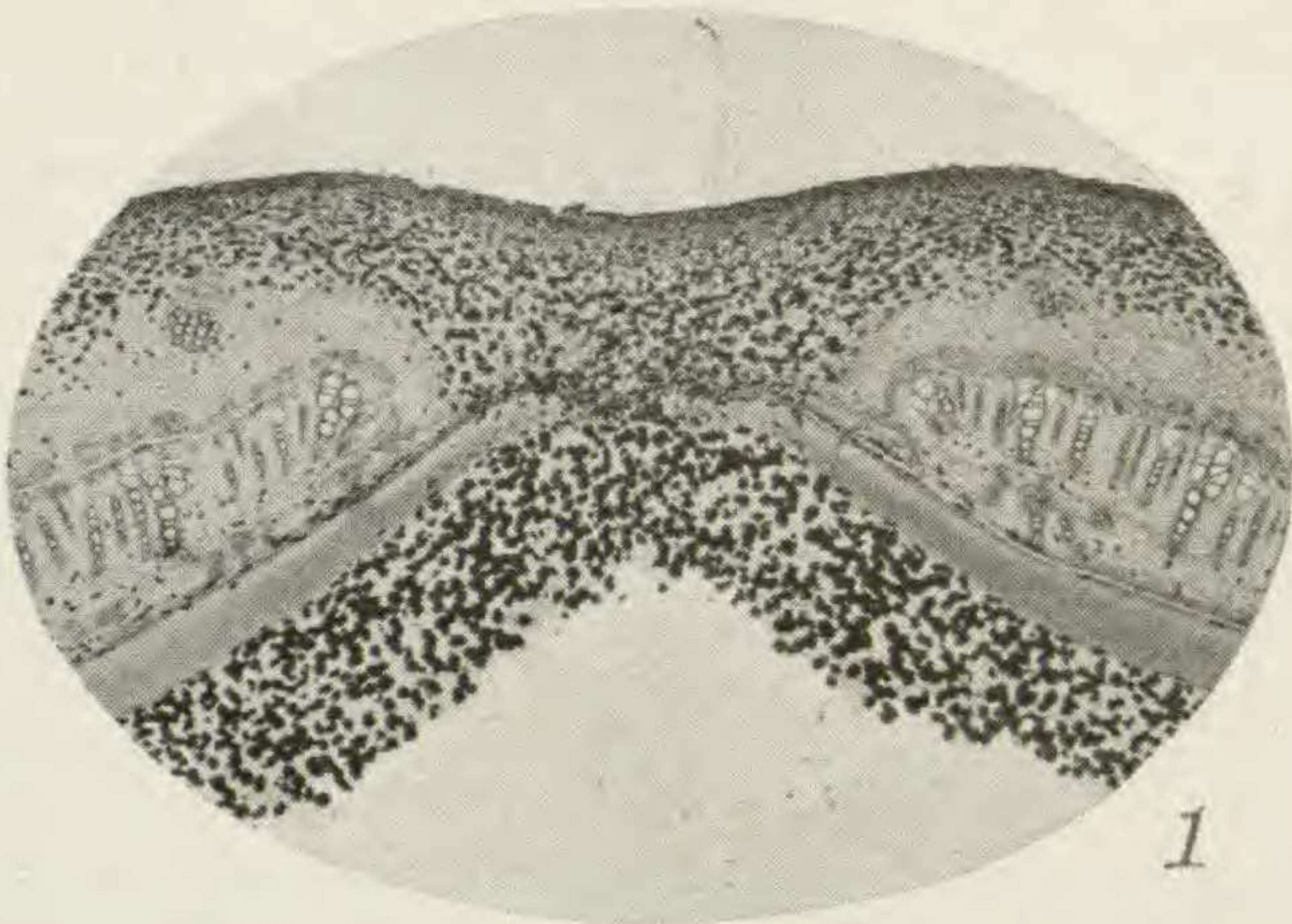
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